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環境条件とそれに対応する生活史特性のパターンについて

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（学位論文題目）

On the Environmental Condition and the Corresponding Patterns of Life History Traits

（環境条件とそれに対応する生活史特性のパターンについて）

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（論文内容の要旨）

生物の行動や生活史パターンを適応や自然選択の立場から考察する理論的研究は，最適化理論やゲーム理論の導入により，近年巾広く展開されてきている。しかし，個体特性と個体間干渉に関係した性質が，ともに自然選択の対象になると思われる生活史パターンの問題は通常の最適化理論やゲーム理論では避け難い難点があって，両方の特性を関連づけて解析した研究は，まだ行なわれていない。

申請者は，この問題をダイナミカル・モデルを基礎にして，進化的安定戦略（ＥＳＳ）の視点から解析する方法を展開している。産卵数，物理的環境条件に対する生存率，種内の個体間競争に対する耐久性をあらわす３つのパラメーターを戦略セットとして，その中で可能ないかなる変異個体ももはや侵入不可能になるための条件，すなわち進化的に安定な戦略を，個体間相互作用を考慮したダイナミカル・モデルに基づいて解析した。ここで考えている戦略セットとしてのパラメーターは，勿論独立に変化するのではなくて，一般的に予想されるある制限条件を課して解析を行っている。

まず，産卵数と物理的環境に対する生存率について変異を考えた場合には，環境条件が厳しくなるほど，ＥＳＳは生存能力を高めて産卵数を減らす方向に変化するし，逆に産卵数と種内競争に対する耐久性についての変異が許される場合には，種内競争に対しては弱くなっても産卵数を増す方向にＥＳＳが変化することを示した。さらに，環境条件と種内競争の厳しさの度合に応じて，この傾向が一般的に成立することを証明している。

さらに，ここで明らかにされた結論に基づいて，これまで多くの研究者の議論の的になってきたマッカーサー・ウィルソンのｒ戦略Ｋ戦略の問題に関するいろいろな説に対する総括的な再検討を行っている。

参考論文では，捕食寄生者のニッチの重なりを考慮して，一種導入と多

種導入のどちらが生物的防除で有利かという問題を数学モデルを用いて解析している。

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（論文審査の結果の要旨）

大卵少産か小卵多産かといった問題をはじめとして，マッカーサー・ウィルソンのｒ戦略Ｋ戦略の問題は多くの研究者の議論の対象になり，いろいろな説が出されているが，種内の個体間干渉まで考慮に入れて，適応や自然選択の立場から解析した理論的研究はまだない。こうした生活史パターンに関係した問題は，通常の最適化理論やゲーム理論では避け難い難点があるためでもある。

そこで，申請者はこの問題をダイナミカル・モデルを基礎にして，進化的安定戦略（ＥＳＳ）の視点から解析する方法を用いた。産卵数，物理的環境条件に対する生存率，種内の個体間競争に対する耐久性をあらわす３つのパラメーターを戦略セットとして，その中で可能ないかなる変異個体ももはや侵入不可能になるための条件，すなわち進化的安定戦略（ＥＳＳ）の条件をダイナミカル・モデルを用いて解析している。

産卵数と物理的環境に対する生存率について変異を考えた場合には，環境条件が厳しくなるほど，ＥＳＳは生存能力を高めて産卵数を減らす方向に変化するが，産卵数と種内競争に対する耐久性についての変異では，逆に，種内競争には弱くなっても産卵数は増す方向にＥＳＳが変化することを示した。さらに環境条件と種内競争の厳しさに応じて，一般的にこの傾向が成立することを証明している。

この研究は，これまで種々の立場からの推論に基づいて議論されてきた未解決の問題に対して，進化的安定戦略の視点から明確な解答を与えたもので，進化生態学での重要な寄与といってよい。

参考論文では，捕食寄生者のニッチの重なりを考慮して，一種導入と多種導入のどちらが生物的防除で有利かという問題を数学モデルを用いて解析しており，申請者の数理生態学の分野での秀れた研究能力を示している。

よって，本論文は理学博士の学位論文として価値あるものと認める。

なお，主論文及び参考論文に報告されている研究業績を中心とし，これに関連した研究分野について試問した結果，合格と認めた。

主論文 1

ON THE ENVIRONMENTAL CONDITION AND THE CORRESPONDING PATTERNS OF LIFE HISTORY TRAITS

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ABSTRACT

Life history evolution is investigated with a mathematical model. The model has three parameters which represent phenotypic variation among individuals of a species. The parameters are (1) clutch size, (2) viability against the (physical) environment, (3) viability against intraspecific competition. The trade-off relation between the three parameters is imposed. The model has one more parameter that represents the intensity of density independent mortality(harshness of the environment). The values of the three parameters are regarded as a strategy. Analysis is made to investigate how the evolutionarily stable strategy(ESS) shifts in accordance with harshness of the environment. First, the model is analyzed in the case where variation only in (1) and (2) is allowed. The result is that the ESS shifts to be less fecund and more viable to the environment as the environment becomes harsher. Second, the case where variation only in (1) and (3) is allowed is analyzed, and the result is that the ESS shifts to be more fecund and less viable to intraspecific competition as the environment becomes harsher. Finally, the case without restrictions is analyzed and the condition for the above two tendencies to be expected is found. The results obtained in this paper are compared with those previously derived from the theories of life history. The general framework for the theory of life history evolution under various situations is also discussed.

INTRODUCTION

When ethologists consider the adaptive significance of a particular behavior of an organism, it would be helpful to see it from the view point of general life history evolution. Behavior of high competitive ability might have evolved in a crowded population because of so called K selection(Pianka, 1970). Horn & Rubenstein(1984) argued that behavioral adjustments of life history are just one kind of channels and that the responses through other channels(physiological, developmental, and genetic adjustments) are also important in behavioral ecology. Theory of life history evolution that yields inferences in terms of demographic parameters(birth and death rates, etc) is far from a direct prediction on behavioral level, but still helpful for investigation in the total context of life history adjustments.

Unfortunetely, most theories of life history evolution so far presented are those of density and/or frequency independent selection(Schaffer,1974; Caswell,1980; Ricklefs,1981;etc). Hence these theories cannot cover social behavior of organisms, because social behavior involves change in fitness due to interference(or, sometimes, cooperation) with other individuals and consequently evolution is under density and frequency dependent selection. On the contrary, study on the evolution under frequency dependent selection has much advanced by the game theoretic approach(see Maynard Smith,

1982 for review). Owing to that, various kinds of social behavior have been successfully understood from natural selection view point. But in these cases, frequency independent part of fitness is taken for granted as common to all individuals and likely to be completely disregarded. So this approach is not sufficient for the investigation on r- and K-selection theory because the theory involves a trade-off between density independent component(r) and density dependent component(K) of fitness.

In this paper, I investigate the patterns of expected life history in relation to the environmental condition under density and frequency dependent natural selection. The relations between the environmental condition and the observed life history have been discussed in various ways. Most famous one may be that of r- vs K-selection proposed by MacArthur & Wilson(1967) and extended by Pianka(1970), which predicts evolution of high r(intrinsic growth rate) in disturbed habitats whereas evolution of high K(carrying capacity) in stable habitats. On the other hand, Itô(1959, 1980) proposed that small clutch size by large eggs has evolved in a harsh environment where the offspring cannot easily feed themselves. This seems at sight to be a contradiction to r- and K-selection theory because it predicts large clutch size must evolve in such an environment where the population does not become crowded. Stearns(1976, 1977) has already pointed out that the terms, r- and K-selection, tend to be easily abused just like

labels, and the wide variety and confusion of the meanings of these terms are well reviewed by Parry(1981). In addition to the above two theories, Grime(1977) proposed three different life history patterns(competitive, stress-tolerant, and ruderal) owing to the distinction between stress and disturbance in environmental conditions. I do not intend here to present a comprehensive review of the studies on life history evolution so far published because there are too much and we already have some good reviews (Southwood, 1977; Horn, 1978; Horn & Rubenstein, 1984; etc). To avoid verbal ambiguity, I make use of a mathematical model in this paper.

The features of the model constructed here is as follows. First, differential competitive ability among individuals is incorporated in addition to difference in density independent mortality. The carrying capacity K itself cannot be an attribute of an individual(Stearns, 1977). The essence of K-selection lies in a differential susceptibility against density effect(Pianka, 1972). Thus, the term K-selection is used in this sense hereafter. Incorporating the difference in competitive ability, the model is necessarily that of density and frequency dependent selection. Defensive and offensive components are distinguished between in the differential competitive ability. Its relevance to the discrimination of α-selection (offensive component) from K-selection by Gill(1974) is also discussed. Second, I seek the evolutionarily stable strategy(ESS; introduced by Maynard Smith & Price, 1973;

well reviewed in Maynard Smith, 1982) based on the above model. A strategy set is set up and the graphic method similar to the Levins'(1968) fitness-set approach is used though our analysis is based upon a population dynamic model and its ESS. Third, the shifts of the ESSs according to the change of the environmental condition is analyzed and compared with the theories of life history evolution so far presented. The result is that the r- and K-selection theory and Itô's theory are independently valid in different and limited situations. What happens in the comprehensive situation is then analyzed and discussed.

The model presented here only covers very simple cases with respect to population structure, but is still illustrative of general cases. A comprehensive framework for the theory of life history evolution under various situations is also discussed.

OUTLINE OF THE APPROACH

The approach adopted here is based on the idea of evolutionarily stable strategy(ESS). A brief review is presented on the conceptual framework of ESS.

Suppose that a certain phenotype is common in the population. If a rare mutant invaded into the population, it might propagate and replace the individuals of the old phenotype. At last, in this way, the population can evolve to the state which allows no other mutant to propagate. The

word 'phenotype' here means any trait that is inherited to the offspring, and includes behavior as well as morphology. So it is often replaced by the word 'strategy', also emphasizing the potential flexibility of a species. The ESS is a strategy that permits no mutant of alternative strategy to propagate if all the members of the population adopt it. The aim of this paper is to investigate the way ESSs change in accordance with the environmental condition.

To make an accurate argument, we must specify the following three things.

(1) a strategy set This is a set of all possible strategies that might arise by mutation. We cannot find an ESS without specifying the range of alternative strategies. A species shows flexibility according to the local habitat condition. The set must cover all such variations. Strategy is often expressed in terms of the parameters that appear in Darwinian fitness of an individual. In other words, parameters in the models of population growth can be interpreted as strategies(Southwood, 1977). In these cases, reasonable strategy sets are usually confined to some regions and do not cover all the parameter spaces. We can expect, say, neither a completely immortal organism nor an organism that produces a large number of large eggs at the same time(there must be a trade-off between these two). Thus the strategy set can be expressed as the subset of parameters upon which constraint is imposed. The detail of the constraint will depend on the species or the design of an organism, which is closely related to developmental

biology.

(2) genetics and mutation 'regime' The genetic system of an organism can affect the observed frequencies of phenotypes. The things are much simpler if the genetic system is haploid asexual. This, unrealistic postulation to real diploid sexual populations, is proved to be useful as a first approximation in many cases(Maynard Smith, 1982).

The way mutation takes place can also affect the predictions of ESSs. Suppose that the ESS is such a strategy that maximizes 'fitness' in some sense. Then, the strategy which corresponds to local maximum of fitness is an ESS if the mutation can only arise near by. But it is no longer an ESS if the mutation can take place anywhere in the strategy set and then replaced by the strategy of the globally maximal fitness.

(3) the relation between a strategy and its fitness Inference about the displacement between strategies (phenotypes) needs to specify the rule that determines the most successful strategy. In most cases so far presented as an application of ESS framework, fitness is defined a priori based upon the idea of Darwinian fitness and the strategy that maximizes the fitness is assumed to be the most successful one. But we cannot simply make use of this method for the cases of density dependent selection. In these cases, Darwinian fitness varies according to the population density and the strategy that maximizes the fitness might be different at different density levels.

Moreover, the fitness is always unity if the population reached the stable steady state. Hence I utilize a model of population dynamics as the rule to determine the successful strategy. In this method, strategies are defined as the parameters involved in the model as mentioned above. Meanwhile, the environmental condition is naturally incorporated in the model as another parameter.

Population dynamical models for competing phenotypes that are haploid asexual are formally the same as those for the community of competing species. So the model is very complicated if the population structure is complex. It is one of the central tasks of ecology to formulate the ups and downs between various 'species' that are interacting in a complex manner. In this paper, I concentrate upon a simple population. The detailed explanation for the model is given in the following section.

MODEL

A simple population considered here is that of haploid asexual and of which generations are nonoverlapping. The extension of the model to the cases of overlapping generations is discussed later. I must note that our consideration here is limited to the cases of fixed life span. Though the assumption of nonoverlapping generations aims at simplification, it holds true for most arthropod species in the temperate zone.

Even in the simple population, organisms interact with

their physical and biological environment and other members of the population in a very complex manner. So we cannot incorporate all the relevant factors into the model. The parameters involved in the model is restricted to be minimal for the investigation on life history evolution under density and frequency dependent selection. They are (i) the number of the offspring per clutch, (ii) the mortality coefficient induced by the environmental factors, and (iii) the mortality coefficient induced by intraspecific competition.

The model used here is given below. The temporal change of the number of individuals of each phenotype is expressed by the equations (1).

$$N_0^{t+1} = m_0 N_0^t \exp(-\varepsilon_0 h)\exp(-a_{00} m_0 N_0^t - a_{01} m_1 N_1^t), \quad (1.0)$$

$$N_1^{t+1} = m_1 N_1^t \exp(-\varepsilon_1 h)\exp(-a_{01} m_0 N_0^t - a_{11} m_1 N_1^t). \quad (1.1)$$

The model of this type has often been used for a monomorphic population($N_1=0$) and its dynamical behavior has been well studied because it involved chaotic behavior for some parameter values(May & Oster, 1976). The two phenotypes are the common one if the subscript is 0($i=0$) and the rare mutant if $i=1$. The variable N_i^t($i=0,1$) represents the adult number of the phenotype i($=0,1$) at the t-th generation. The meaning of the parameters is as follows: m_i denotes the clutch size(number of offspring per

adult), h represents the environmental condition(harshness of the habitat), and ϵ_i is a sensitivity coefficient against the harshness. The factor $\exp(-\epsilon_i h)$ represents the survival rate due to density and frequency independent mortality. Note that the survival rate decreases as the harshness(h) increases, and that the decrease caused by the harshness is more remarkable if the coefficient ϵ_i is larger. In this sense, we can call ϵ_i a fragility of the organism against harshness of the habitat. The parameter a_{ij} denotes competitive coefficient of the phenotype i induced by an individual of the phenotype j. The factor $\exp(-a_{i0}m_0N_0^t-a_{i1}m_1N_1^t)$ then represents the survival rate due to the density and frequency dependent mortality. The reason the term is $a_{ij}m_jN_j^t$ instead of $a_{ij}N_j^t$ is that the competition is performed among the offsprings, not among adults.

I furthermore put a postulation on the competition coefficients. It is that the coefficient a_{ij} can be decomposed into the product of the two components as follows:

$$a_{ij} = k_i\alpha_j \ , \tag{2}$$

where k_i and α_j are the deffensive and the offensive components respectively as explained below. Under this assumption, the survival rate due to density and frequency dependence in the equation (1) is replaced to alter the model as follows:

$$N_i^{t+1} = m_i N_i^t \exp(-\varepsilon_i h)\exp(-k_i C^t), \qquad (3)$$

where we defined

$$C^t = \sum_{j=0}^{1} \alpha_j m_j N_j^t \ . \qquad (4)$$

The quantity C^t represents the degree of crowdedness in the population at the t-th generation since it is a weighted sum of all offsprings at the time. The phenotype specific weights(α_js) can be regarded as an offensive component because the individual of a larger weight increases density dependent mortality of the others more than that of a smaller one does. On the contrary, we can interpret k_i to be a susceptibility coefficient against the crowdedness. The individuals of a larger susceptibility coefficient suffer higher density dependent mortality than those of a smaller one. Hence this coefficient can be taken as defensive component. Mathematical consequence of the postulation (2) is that it excludes the cases of coexistence of the two phenotypes except for the case where the two are 'identical'(i.e., $\ln m_0 - \varepsilon_0 h = \ln m_1 - \varepsilon_1 h$, $k_0 = k_1$).

ANALYSIS AND RESULTS

In the model (3) with (4), what kind of strategy(i.e.

parameters) turns out to be evolutionarily stable after successive invasions of possible mutants? I first examine whether or not the phenotype 1 can invade the monomorphic population of the phenotype 0. To this end, we now illustrate the change of Darwinian fitness(ϕ_i) in relation to the degree of crowdedness(C). The lines in Fig.1 represent those of the phenotype 0 and the phenotype 1:

$$\ln \phi_0 = \ln m_0 - \varepsilon_0 h - k_0 C, \tag{5.0}$$

$$\ln \phi_1 = \ln m_1 - \varepsilon_1 h - k_1 C. \tag{5.1}$$

We can see that the phenotype of higher Darwinian fitness is different at different levels of C in this case. Since population growth stops when $C=C_i^*$ such that $\phi_i(C_i^*) = 1$ ($\ln \phi_i(C_i^*) = 0$), the saturation crowdedness of the population consisting only of the phenotype i, C_i^*, is given as follows:

$$C_i^* = (\ln m_i - \varepsilon_i h)/k_i. \tag{6}$$

The phenotype 1 can invade into the population of the phenotype 0 if its Darwinian fitness is larger than unity(i.e. $\ln \phi_1 > 0$) at such a level of the crowdedness of the phenotype 1:

$$\ln \phi_1 = \ln m_1 - \varepsilon_1 h - k_1 C_0^* > 0. \tag{7}$$

This condition can be rewritten as follows:

$$\frac{\ln m_1 - \varepsilon_1 h}{k_1} \left(= C_1^*\right) > C_0^* = \frac{\ln m_0 - \varepsilon_0 h_0}{k_0} \qquad (8)$$

In this way, it is suggested that the population is finally occupied exclusively by the phenotype of maximal C^*. In the rough reasoning above, I assumed that the population is stable at crowdedness level C_0^*. But the condition (8) for the mutant to be able to propagate holds even in such a case where C_0^* is unstable(mathematical proof is given in Appendix 1). Thus we can conclude that C^* always increases and is finally maximized in the model (3). What is maximized is not K but C^*. This is consistent with the proposition in Iwasa & Teramoto (1980):the number of individuals at the stage in which they are exposed to the strongest competition is most likely to be maximized. We should note here that C^* is independent of α as shown in the equation (6). A atrategy that adopts more aggresive bahavior which corresponds to larger α can be expected to have smaller m or larger k, ε that results as to smaller C^*. Hence it concludes that, in model (3), aggresive behavior will not evolve. Thus α is omitted from strategy parameters in the analysis of the model (3). Note that the absence of evolution of aggresive behavior in model (3) is based on the assumption that each individual suffers density dependent mortality due to himself, which is explained in detail in discussion.

(i) CLUTCH SIZE(m) VS FRAGILITY AGAINST THE ENVIRONMENT(ε)

First of all, we examine the case where only the clutch size(m) and the fragility against the environment(ε) are strategy parameters, upon which trade-off relation is imposed. The susceptibililty against crowdedness(k) is kept constant in this case(i.e. $k_i \equiv k$). It is reasonably expected that, if the clutch size decreases, each offspring suffers less mortality owing to increased allocation of resource per individual. For example, increase in egg size might result this way. This means the clutch size increases as the fragility of each individual increases. Thus the trade-off relation(constraint) is that m is a monotonically increasing function of ε. One example of such relations is drawn in (m,ε) space as a bold curve(Fig.2(a)). Meanwhile, the contours of C can be superimposed in the same space as parallel lines with slope h because, from the equation (9), we have

$$\ln m = \varepsilon h + kC^{*}, \qquad (9)$$

provided that m is scaled logarithmically. In Fig.2(a), we can find graphically the ESS as a point at which the constraint curve is tangent to one of the contours. Moreover, to be ESS, the constraint curve must be concave at the point. Then, how does the ESS shift if the environment becomes harsher? As h gets larger, the contours become steeper and, consequently, the ESS shifts to the

left on the constraint curve(Fig.2(b)). This implies that a smaller clutch size turns out to be ESS. The shift of ESSs is saltatory for a particular type of the constraint curves(Fig.2(c)). Even in this case, the tendency that a harsher environment favors smaller clutch size remains unchanged. Saltatory shift cannot happen, if the mutation is restricted to arise near by.

Itô(1959, 1980) has claimed that a small clutch size seems to have evolved in the environment where it is difficult for the offspring to get food, opposing to the r- and K-selection theory. If the difficulty in getting food is only caused by the nature of the resource in the environment(not due to intraspecific competition), we can regard this as the harshness of the environment(i.e. density independent mortality). In this sence, the prediction of the model supports Itô's statement. Nevertheless his theory does not contradict to that of the r- and K-selection. If we keep k to be constant, the maximization of C^* coincides with that of r:

$$r = \ln m - \varepsilon h. \qquad (10)$$

Thus the prediction made here lies within r-selection, in other words, b(birth) versus d(death) selection(Pianka, 1972). It is different from r- vs K-selection view point.

(ii) CLUTCH SIZE(m) VS SUSCEPTIBILITY AGAINST THE

CROWDEDNESS(k)

In this section, we examine the case where only the clutch size(m) and the susceptibility against the crowdedness(k) are strategy parameters, upon which trade-off relation is imposed. The fragility to the environment (ε) is kept constant here(i.e. $\varepsilon_i \equiv \varepsilon$). In this case, it seems reasonable to postulate that the increase in clutch size results as a reduced competitive ability of each offspring. This means m increases as k(susceptibility) becomes larger. Again, we assumed that the trade-off relation is a monotonously increasing function. One such example is drawn in (m, k) space as a bold curve(Fig.3(a)). But the contours are slight different from the previous case. They are lines that have common m-sections, εh:

$$\ln m = \varepsilon h + kC^{*}. \qquad (11)$$

The ESS is, as before, a point at which the constraint curve is concave and tangent to one of the contours(Fig.3(a)). In this case, the ESS shifts to the right if the environment becomes harsher(h increases) (Fig.3(b)). It means that the clutch size increases at the expense of competitive ability as the environment becomes harsher. Saltatory shift of ESS can also take place for a particular type of the constraint curves(Fig.3(c)). The tendency stated above still holds in such a case. This is quite consistent with the commonly held view of r- and K-selection. It should be emphasized that the relationship is

now based on ESS.

(iii) COMPREHENSIVE SITUATION

What will happen if we take three parameters, m, ε, and k, as a strategy? In this case, increase in m does not always accompany increase in ε(or k). At the expense of k(or ε), m can increase with decreasing ε(or k) at the same time. But, as a constraint(trade-off relation), we can expect increase in m as ε or k increases for fixed k or ε respectively:

$$m = \hat{m}(\varepsilon, k), \tag{12}$$

where

$$\frac{\partial \hat{m}}{\partial \varepsilon}(\varepsilon, k) > 0, \quad \frac{\partial \hat{m}}{\partial k}(\varepsilon, k) > 0. \tag{13}$$

The ESS is the strategy that maximizes C^* given in the equation (6). We can make use of a graphical method in three dimensional (m, ε, k) space as before. But we cannot easily see, in this case, the shift of ESSs in relation to the environmental condition. Hence we use an analytical method. The detail of the analysis is given in Appendix 2. For each h, we will have a parameter value ($\varepsilon^*(h)$, $k^*(h)$, $\hat{m}(\varepsilon^*(h), k^*(h))$) that is ESS. From Appendix 2, we have

$$\frac{d\varepsilon^*}{dh} < 0, \quad \frac{dk^*}{dh} > 0, \tag{14}$$

provided that

$$\frac{\partial^2 \hat{m}}{\partial \varepsilon \partial k} < 0. \qquad (15)$$

This condition (15) implies that the increase of m at the expense of unit ε for fixed k(i.e.$\frac{\partial \hat{m}}{\partial \varepsilon}$) decreases as k increases. This is a sufficient condition for the inequalities (14) to hold. We also have, from (12),

$$\frac{dm^*}{dh} = \frac{\partial \hat{m}}{\partial \varepsilon}\frac{d\varepsilon^*}{dh} + \frac{\partial \hat{m}}{\partial k}\frac{dk^*}{dh}. \qquad (16)$$

The inequalities (14) imply that the tendencies predicted in (i) and (ii) hold if we disregard the change in m. On the contrary, whether or not m^* increases as h becomes larger is affected by the partial derivatives as shown in (16). If the increase in ε produces more increase in $\hat{m}$ than that in k does($\frac{\partial \hat{m}}{\partial \varepsilon}$is larger than $\frac{\partial \hat{m}}{\partial k}$), $\frac{dm^*}{dh}$ tends to decrease as h gets larger, and vice versa. In other words, which of the tendencies, those of Itô's and r- and K-selection, actually observed in the population depends critically on the constraint of the species.

Grime(1977) distinguished two different environmental conditions, disturbance and stress. From our point of view, stress is a mortality that can be reduced by the effort of the species, while disturbance is not. Then, in the cases where only the degree of disturbance varies, the species must adapt adjusting the trade-off between m and k because ε has little effect on maximization of C^*. In these cases, the situation is as presented in (i) and the result is consistent with Grime's ruderal vs competitive strategies. On the other hand, in the cases where only the degree of

stress varies, the situation is as presented in (iii). As predicted by the inequalities (14), ESS becomes more stress-tolerant(smaller ε^*) and less competitaive(larger k^*), which is consistent with the Grime's assertion.

DISCUSSION

Social structure of the population is involved in the functional form of density effect. In this paper, the form is limited to the exponential one. This corresponds to the scramble type, in which almost none survives when the initial density is excessively high(Hassell, 1976). The other typical one is the contest type, in which constant number of individuals survive even at excessively high density. An example of the population growth model for the contest type is as follows:

$$N_i^{t+1} = m_i N_i^t \exp(-\varepsilon_i h) \frac{1}{1 + k_i \sum_j \alpha_j m_j N_j^t}. \qquad (17)$$

Are the predictions given in the previous section affected by such social structures? It is already revealed that they hold true for a wider class of functional forms of density effect, including the one in (17) (Kakehashi & Nakajima, in preparation). Thus the results obtained here are rather universal ones.

In the model (3) with (4), an individual suffers density dependent mortality due to himself. This will hold

if the competition is exploitative one, but will not if it is interference one. In the latter case, the model should be modified by excluding his own effect out of the density dependent mortality term as follows:

$$N_i^{t+1} = m_i N_i^t \exp(-\varepsilon_i h)\exp(-k_i \sum_{j=0}^{1} \alpha_j (m_j N_j^t - \delta_{ij})), \quad (18)$$

where $\delta_{ij}=1$ if $i=j$ and $\delta_{ij}=0$ if $i\neq j$. The equation (18) can be rewritten as

$$N_i^{t+1} = m_i N_i^t \exp(-\varepsilon_i h)\exp(k_i \alpha_i)\exp(-k_i C^t), \quad (19)$$

where C^t is the same as defined in (4). Gill(1974) pointed out that α-selection must be distighuished from K-selection because high competitive ability in α-selection implies reduction of other individual's fitness and it is related to interference competition. On the contrary, high competitive ability in K-selection means high saturation density(or carrying capacity, K) and it is related to exploitative competition. In our models, K_i(carrying capacity of the monomorphic population of phenotype i) is given as the equation (20) below:

$$K_i = \frac{\ell n\, m_i - \varepsilon_i h}{m_i k_i \alpha_i} \ (+1), \quad (20)$$

where '+1' is only necessary for the model (18). We see the phenotype of high competitive ability in defensive

component(small k) has a large K and that in offensive component(large α) has a small K. Thus we must regard K-selection as a selection for high competitive ability in defensive component(small k). In the model (18), C^* is also maximized after successive invasions of possible mutants while C^* depends on α as follows:

$$C_i^* = (\ln m_i - \epsilon_i h) / k_i + \alpha_i . \qquad (21)$$

Thus there is a basis for evolution of aggresive behavior. This is consistent with Gill's(1974) criticism. But it is based upon the effect of only one individual and may be negligible if $m_j N_j$s are large. If the interference competition is performed in small subgroups, the effect of one individual cannot be disregarded. In such a case, the formulation of the model (18) can be applicable provided that the between subgroup variance of phenotypic composition is small. As the application of model (18) is limited, the detailed analysis of it was omitted here. As mentioned before, the absence of evolution of aggresive behavior in model (3) is based on the assumption that each individual suffers density dependent mortality due to himself.

The intrinsic growth rate, r, is also a function of generation time though our consideration is confined to variation of r due to clutch size and survival rate. The model presented here can be extended to the cases where the alternative strategy is a biennial or perennial one, i.e.,

the cases of overlapping generations. The analogous result (maximization of the crowdedness, etc) can be obtained as far as the reproduction is semelparous (monocarpic).

Levins(1968) proposed a graphical method well known with a term, a fitness set. In his theory, he concentrated upon some continuous trait(x) and its fitness is assumed to be $W_1(x)$ and $W_2(x)$ in two different environment, 1 and 2. So we can draw a curve parameterized by x (a fitness set) in (W_1, W_2) space. Let the frequencies of the two environment be p_1 and p_2. Then, he argues the overall fitness of the strategy that adopts (W_1, W_2) is given as $\phi=p_1W_1+p_2W_2$ if the situation is fine grained and $\phi=W_1^{p_1}W_2^{p_2}$ if coarse grained. The contours of ϕ can be superimposed on the (W_1, W_2) space and we can find the optimal strategy graphically. He further discussed on the mixed strategy and polymorphism. The method used in this paper is similar to this but not the same. In fact, the two methods share general features in common. (1) The basic space is spanned by fitness components. (2) The fitness set is a subspace of the basic space, which is an image of the strategy set. In our method, the strategy set is implicit because we defined it in terms of the fitness component from the outset. (3) There is an adaptive function of fitness components which is to be maximized and its contours can be superimposed on the same space. In Levins' case, it was based on the Darwinian fitness(density and frequency independent selection). In our case, it was a degree of crowdedness of

the population. As mentioned in the analysis in (i), the maximization of the crowdedness coincides with that of r(i.e. density and frequency independent component of fitness) if we disregard the difference in competitive ability. In this way, our adaptive function includes density and frequency independent selection as a special case. How the fitness components are integrated into the adaptive function represents the patterns of life history of the species in its environment. The concepts of coase grained and fine grained are represenatives of such patterns. Thus the framework discussed here might be useful in recognizing clearly the various patterns of life histories.

The theoretical studies of density dependent selection was originated from the proposal of K-selection by MacArthur(1962). Roughgarden(1971) then discussed on it by the mathematical model of competing phenotypes in the population. The model involved a trade-off relation though the possible strategies were only a few. Besides, the natural mechanism of the model that determines the population level of crowdedness was neglected and the level was arbitarily set from outside of the model. In our approach, the strategy set is improved to be fully specified and the level of crowdedness is determined by the model itself. But the predictions are still concerned with the same species. The theories on relationships between the environmental condition and the life history patterns have also been discussed by comparison between species. The

introduction of the constraint of the species in this paper might provide the definite basis for the theory of interspecific relationships of the life history patterns. Saltatory shifts of ESS might have something to do with it.

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REFERENCES

Caswell, H. 1980 On the eguvalence of maximizing reproductive value and maximizing fitness. Ecology 61:19-24.

Gill, D.E. 1974 Intrinsic rate of increase, saturation density and competitive ability. II. The evolution of competitive ability. Amer. Natur. 108:103-116.

Grime, J.P. 1977 Evidence for the existence of three primary strategies in plants and its relevance to

ecological and evolutionary theory. Amer. Natur. 111:1169-1194.

Hassell, M.P. 1976 The dynamics of competition and predation. Studies in biology no. 72, Edward Arnold, London.

Horn, H.S. 1978 Optimal tactics of reproduction and life history. In J.R.Krebs & N.B.Davies(eds.) Behavioural Ecology, 411-429. Blackwell Scientific Publications, Oxford.

Horn, H.S. & D.I.Rubenstein 1984 Behavioral adaptations and life history. In J.R.Krebs & N.B.Davies(eds.) Behavioural Ecology 2nd ed., 279-298. Blackwell Scientific Publications, Oxford.

Itô, Y. 1959 Hikaku seitaigaku, Iwanami Shoten, Tokyo.(in Japanese)

Itô, Y. 1980 Comparative ecology(edited and translated by J. Kikkawa, English edition from the 2nd edition of the book above), Cambridge University press, Cambridge.

Iwasa, Y. & E. Teramoto 1980 A criterion of life history evolution based on density dependent selection, J. theor. Biol. 84:545-566.

Levins, R. 1968 Evolution in changing environments. Princeton University Press, Princeton.

MacArthur, R.H. 1962 Some generalized theorems of natural selection. Proc. Nat. Acad. Sci.(USA) 48:1893-1897.

MacArthur, R.H. & E.O.Wilson 1967 The theory of island biogeography. Princeton University Press, Princeton.

May, R.M. & G.F.Oster 1976 Bifurcations and dynamic complexity in simple ecological models. Amer. Natur. 110:573-599.

Maynard Smith, J. 1982 Evolution and the theory of games. Cambridge University Press, Cambridge.

Maynard Smith, J. & G.R.Price 1973 The logic of animal conflict. Nature 246:15-18.

Parry, G.D. 1981 The meaning of r- and K-selection. Oecologia 48:260-264.

Pianka, E.R. 1970 On r- and K-selection. Amer. Natur. 104:592-597.

Pianka, E.R. 1972 r and K selection or b and d selection? Amer. Natur. 106:581-588.

Ricklefs, R.E. 1981 Fitness, reproductive value, age structure, and the optimization of life-history patterns. Amer. Natur. 117:819-825.

Roughgarden, J. 1971 Density-dependent natural selection. Ecology 52:453-468.

Schaffer, W.M. 1974 Selection for optimal life histories: the effects of age structure. Ecology 55:291-303.

Southwood, T.R.E. 1977 Bionomic strategies and population parameters. In R.M.May (ed.) Theoretical ecology Principles and applications. Blackwell Scientific Publications, Oxford.

Stearns, S.C. 1976 Life-history tactics: A review of the ideas. Quart. Rev. Biol. 51:3-47.

Stearns, S.C. 1977 The evolution of life history traits: A

critique of the theory and a review of the data. Ann. Rev. Ecol. Syst. 8:145-171.

APPENDIX 1

I present here the proof for the proposition that the degree of crowdedness C^*(defined by the equation(9)) always increases in evolution.

Proof) From the equation (3), we have,

$$(N_0^{t+1})^{1/k_0} = (N_0^t)^{1/k_0} \exp[(\ln m_0 - \varepsilon_0 h)/k_0 - C^t], \quad (A1.0)$$

$$(N_1^{t+1})^{1/k_1} = (N_1^t)^{1/k_1} \exp[(\ln m_1 - \varepsilon_1 h)/k_1 - C^t]. \quad (A1.1)$$

Dividing sides by sides, we have,

$$M^{t+1} = M^t \exp(C_0^* - C_1^*), \quad (A2)$$

where $M^t = (N_0^t)^{1/k_0}/(N_1^t)^{1/k_1}$ and $C_i^* = (\ln m_i - \varepsilon_i h)/k_i$.
Hence,

$$\lim M^t = \begin{cases} 0 & (\text{if } C_0^* < C_1^*), \\ \infty & (\text{if } C_0^* > C_1^*). \end{cases} \quad (A3)$$

It is evident that $\{N_0^t\}$, $\{N_1^t\}$ are bounded(never tend to infinity). Thus, $M^t \to 0$ implies $N_0 \to 0$(common type extincts) and $M^t \to \infty$ implies $N_1^t \to 0$(mutant type extincts). The above concludes that the phenotype of larger C^* always replaces that of smaller C^*. Note that this proof is valid even in the case where the population is unstable at C^*. QED.

APPENDIX 2

The reason two tendencies predicted by Itô's and r- and K-selection theories still hold(i.e.(14)) in the comprehensive situation is presented below under the condition (15).

First, we put constraint as

$$\ln m = \ln \hat{m}(\varepsilon, k) = M(\varepsilon, k). \tag{A4}$$

What to be maximized is

$$C^* = (M(\varepsilon, k) - \varepsilon h)/k = C(\varepsilon, k, h). \tag{A5}$$

Since ESS is a strategy (ε^*, k^*) that maximizes C^*, we have, differentiating (A5) by l and k,

$$\frac{\partial C}{\partial \varepsilon} = \frac{1}{k}\left(\frac{\partial M}{\partial \varepsilon} - h\right) = 0, \tag{A6.1}$$

$$\frac{\partial C}{\partial k} = \frac{1}{k}\left(\frac{\partial M}{\partial k} - C\right) = 0. \tag{A6.2}$$

The equations (A6) implicitly defines ESS (ε^*, k^*) as a function of h: $(\varepsilon^*(h), k^*(h))$. Moreover, (A7) below is required for the (ε^*, k^*) to be ESS.

$$\left.\frac{\partial^2 C}{\partial \varepsilon^2}\right|_* = \frac{1}{k^*}\left.\frac{\partial^2 M}{\partial \varepsilon^2}\right|_* < 0, \tag{A7.1}$$

$$\left.\frac{\partial^2 C}{\partial k^2}\right|_* = \frac{1}{k^*}\left.\frac{\partial^2 M}{\partial k^2}\right|_* < 0, \tag{A7.2}$$

and

$$\left(\left.\frac{\partial^2 C}{\partial \varepsilon \partial k}\right|_*\right)^2 - \left.\frac{\partial^2 C}{\partial \varepsilon^2}\right|_* \left.\frac{\partial^2 C}{\partial k^2}\right|_* = \frac{1}{k^{*2}}\left\{\left(\left.\frac{\partial^2 M}{\partial \varepsilon \partial k}\right|_*\right)^2 - \left.\frac{\partial^2 M}{\partial \varepsilon^2}\right|_* \left.\frac{\partial^2 M}{\partial k^2}\right|_*\right\} < 0, \tag{A7.3}$$

where $|_*$ means the derivatives are evaluated at (ε^*, k^*).

Differentiating (A6) by h and solving the linear equations of $\frac{d\varepsilon^*}{dh}$ and $\frac{dk^*}{dh}$,

$$\frac{d\varepsilon^*}{dh} = \frac{1}{k^*\Delta}\left(k^* \left.\frac{\partial^2 M}{\partial k^2}\right|_* + \varepsilon^* \left.\frac{\partial^2 M}{\partial \varepsilon \partial k}\right|_*\right), \tag{A8.1}$$

$$\frac{dk^*}{dh} = \frac{-1}{k^*\Delta}\left(k^* \left.\frac{\partial^2 M}{\partial \varepsilon \partial k}\right|_* + \varepsilon^* \left.\frac{\partial^2 M}{\partial \varepsilon^2}\right|_*\right), \tag{A8.2}$$

where

$$\Delta = \left.\frac{\partial^2 M}{\partial \varepsilon^2}\right|_* \left.\frac{\partial^2 M}{\partial k^2}\right|_* - \left(\left.\frac{\partial^2 M}{\partial \varepsilon \partial k}\right|_*\right)^2 > 0. \tag{A8.3}$$

If $\left.\frac{\partial^2 M}{\partial \varepsilon \partial k}\right|_* < 0$, we have $\frac{d\varepsilon^*}{dh} > 0$ and $\frac{dk^*}{dh} < 0$, (A9)

because of (A7.1) and (A7.2).

What remained is to show $\frac{\partial^2 M}{\partial \varepsilon \partial k} < 0$.

$$\frac{\partial^2 M}{\partial \varepsilon \partial k} = \frac{\partial}{\partial \varepsilon}\frac{\partial}{\partial k}\left[\ln \hat{m}(\varepsilon, k)\right] = \frac{\partial}{\partial \varepsilon}\left[\frac{1}{\hat{m}}\frac{\partial \hat{m}}{\partial k}\right]$$

$$= -\frac{1}{\hat{m}^2}\frac{\partial \hat{m}}{\partial \varepsilon}\frac{\partial \hat{m}}{\partial k} + \frac{1}{\hat{m}}\frac{\partial^2 \hat{m}}{\partial \varepsilon \partial k} < 0.$$

This holds under the assumptions of (13) and (15). QED.

LEGENDS TO FIGURES

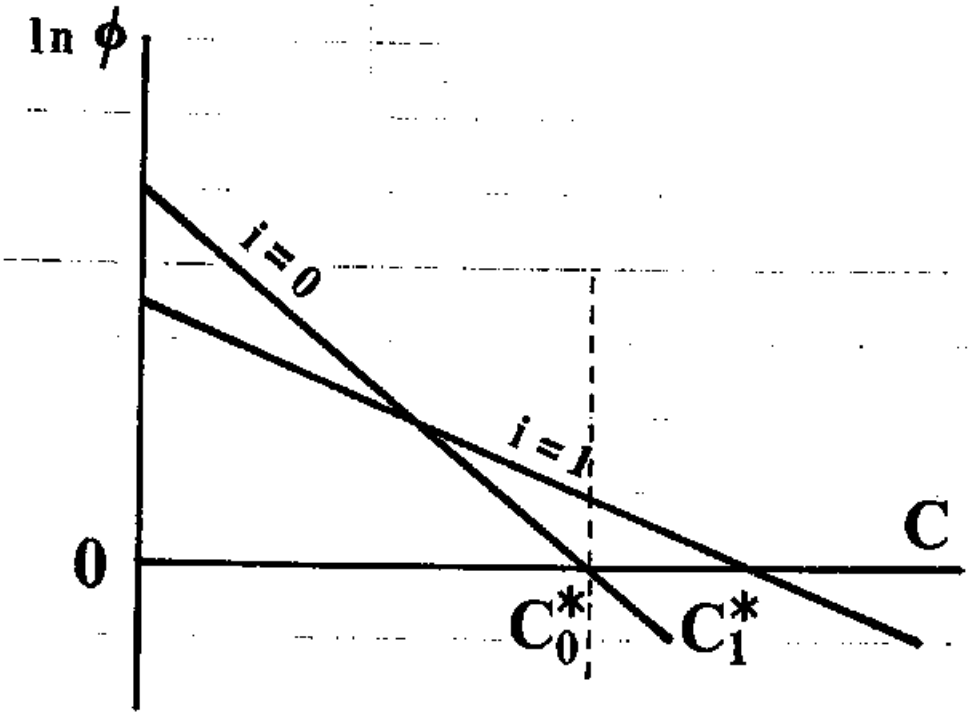
Fig.1. The value of the fitness(ϕ) of each phenotype(i=0, 1) in relation to the crowdedness of the population(C). The fitness of the common type(i=0) intersects the C-axis at C_0^* , which is the equilibrium crowdedness of phenotype 0 population. If the fitness of the mutant(i=1) runs above at $C=C_0^*$, it can propagate because its fitness is higher than the common type. It finally replaces the old phenotype. If it runs below, it cannot propagate.

Fig.2. Analysis of (i) clutch size(m) vs flagility against the environment(ε). (a) The bold curve which is monotonically increasing represents the trade-off relation between m and ε, i.e. the constraint. The parallel lines are the contours of the crowdedness(C). Note that the vertical axis, m, is presented in logarithmic scale. The value of C is larger as m becomes larger. The ESS which is defined as such a point that maximizes C on the constraint curve is found out as indicated by the full circle. (b) As the environment becomes harsher, the contours turn out to be steeper. Then the ESS shifts to a less fecund strategy. (c) Saltatory shifts take place for particular types of the constraint curves. Even in such cases, the relationship exhibited in (b) still holds true.

Fig.3. Analysis of (ii) clutch size(m) vs susceptibility against the crowdedness(k). (a) The bold curve is the trade-off relation between m and k. The vertical axis is logarithmically scaled. The lines of common m-section are the contours of C, where a line of steeper slope corresponds to a larger C value. The ESS, at which C is maximized , is found out as the full circle. (b) As the environment becomes harsher, the contours' m-section turns out to be higher. Thus the ESS shifts to a more fecund strategy. (c) Saltatory shifts are predicted for particular types of constraint curves. Even in such cases, the relationship exhibited in (b) is kept unaltered.

Fig. 1

Fig. 1



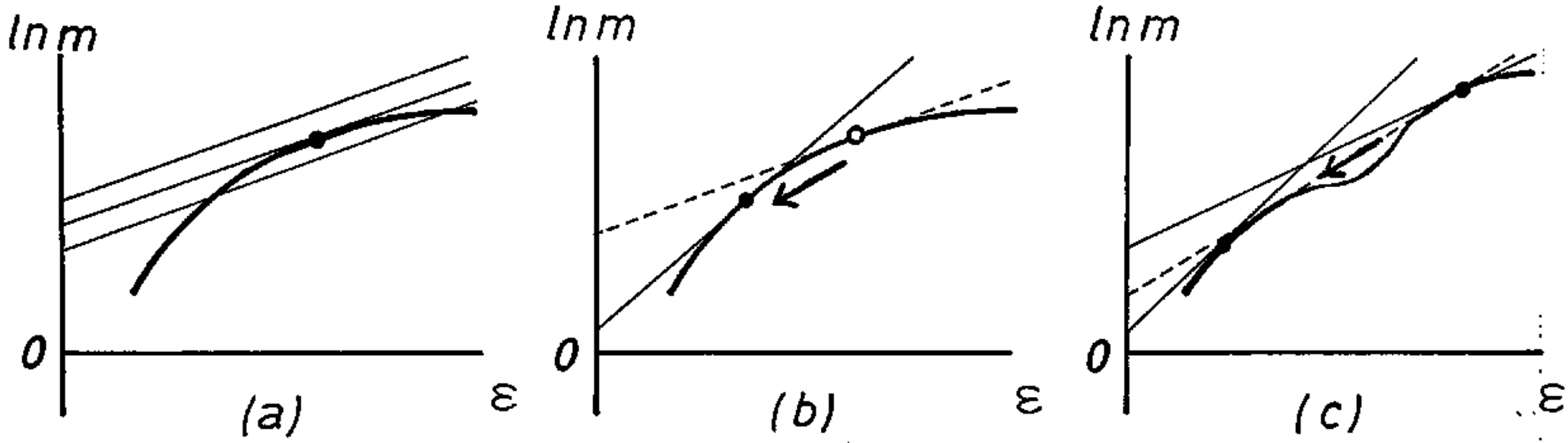


Fig. 2

Fig. 3